PAN-PACIFIC ENTOMOLOGIST
61(2), 1985, pp. 95–104

Predatory and Mating Behavior of *Stichopogon* (Diptera: Asilidae) in Arizona

LES WEEKS AND HENRY A. HESPENHEIDE

(LW) Department of Geography, University of California, Los Angeles, California 90024; (HAH) Department of Biology, University of California, Los Angeles, California 90024.

Abstract.—*Stichopogon catulus* O.S. was studied along Cave Creek Canyon below Sunny Flat Campground, Chiricahua Mountains, Arizona, in late May and early June of 1980. Censuses of individuals along ¼ mi of stream show diurnal changes in activities and locations of the flies: Feeding is more common in the morning than in the afternoon; intraspecific interactions, including copulation, are more frequent in the afternoon than morning; flies are more frequent away from the stream very early and late in the day and move to rocks in the stream during midday periods. Flies orient toward the sun. No courtship was observed, but females signal unwillingness to copulate by raising their abdomen. Copulations last as long as 16 min and interruptions are often attempted by a second male, in one case successfully. Foraging sallies are usually for prey in the air, but occasionally for prey on the water surface, especially for water strider nymphs. Prey are usually Diptera (73%) or Hemiptera (11%) and average 2.8 mm in length (range: 1.5–5.5 mm); females are more frequently seen with prey than are males. *Stichopogon trifasciatus* (Say) was observed near Portal in August 1980. In this species, courtship may or may not precede an attempted copulation by a male, which makes the species especially interesting for study of the effectiveness of courtship.

Stichopogon is a small genus in the Dasypogoninae with 10 species found in North America north of Mexico (Martin and Wilcox, 1965), all but one of which were characterized in a key given by Wilcox (1936) in the most recent and comprehensive treatment of the genus. Except for the widespread *S. trifasciatus* (Say), whose biology was described by Lavigne and Holland (1969), the species are poorly known.

The family Asilidae in the Cave Creek Canyon area of the Chiricahua mountains of southeastern Arizona has been extensively collected, and Alcock (1974), Hespenheide and Rubke (1977) and Linsley (1960) have published studies of members of the family present there. During visits to the Canyon during the spring and summer of 1980 and 1981 small populations of *S. trifasciatus* and relatively large ones of *S. catulus* Osten Sacken were discovered and observed; *S. fragilis* Hine occurs nearby. This paper will primarily treat the population of *Stichopogon catulus* which was studied for several aspects of its behavior: temporal patterns in local population size, levels of foraging and reproductive behavior, intraspecific interactions, perch sites, and orientation with respect to the sun. Prey items were

recovered and analyzed, and qualitative observations made of this species' reproductive, foraging, and general behavior. Notes were also made on the courtship behavior of *S. trifasciatus* which supplement those of Lavigne and Holland (1969) for that species.

Study Sites, Organisms, and Methods

S. catulus was observed between 24 May and 9 June 1980 along Cave Creek adjacent to and downstream from Sunny Flat campground in the lower part of Cave Creek Canyon in the Coronado National Forest, Cochise County, Arizona. The campground is located approximately 3.4 mi southwest of Portal at about 5400 ft elevation. Flies were observed and collected along a ¼ mi section of stream and regularly censused along a portion approximately 2.5 m wide and 65 m in length. At the census site the stream is bordered by a steep embankment (approx. 1.25 m high) on its south side and dry riverbed consisting of cobble to boulder-sized granitic rocks (1–5 m wide) on its north side. During the course of the observations the stream was 0.1–0.75 m deep where running, with an approximate average depth of 0.25 m, and was fast-moving with many riffles and exposed granitic boulders 0.2–1 m in diameter. This part of the canyon is characterized on its south and north sides by very high and steep rock cliffs which cast long shadows in the late afternoon. Vegetation bordering and in places overhanging the stream consists primarily of sycamores (*Platanus wrightii*), some oaks (*Quercus* spp.), alligator junipers (*Juniperus deppeana*), and willows (*Salix* sp.) which grow to heights of 3–25 m. The effect of their shadows is very noticeable in the afternoons, when by 1630 hr MST the entire census strip is in shade.

S. trifasciatus was observed and collected regularly during August 1980 in Silver Creek about 1 mi west of Portal along the road to Paradise at an elevation of about 4880 feet. The wash is relatively densely populated by shrubs of the genus *Chrysothamnus*; vegetation surrounding the wash is a mixture of *Prosopis juliflora, Acacia constricta,* and *Mimosa biuncifera* with a few scattered walnuts and junipers. Courtship behavior was studied there on August 21st between 925 and 1002 hr MST. The species was also collected in nearby Hidalgo County, New Mexico, about 30 mi south of Animas.

S. catulus was redescribed by Wilcox (1936) and is characteristically elongate in shape, dark grayish-black in color, and sexually dimorphic in size (average male length, 5.60 mm, $n = 27$; average female length, 6.99 mm, $n = 31$). In addition to being smaller, males have an overall gray coloration with a whitish-silvery mystax and with pollinose portions of the thorax and abdomen pale grey. The female is noticeably larger and more yellowish in coloration, including a yellow-gold mystax and more yellowish or pale brown pollinose areas. Throughout the study individuals were only seen perched on rocks in and adjacent to Cave Creek. *S. trifasciatus* is a widespread and abundant species, considerably larger in size (mean length 13.00 mm, $n = 6$) and without the sexual dimorphism in size or coloration found in *S. catulus*; it is included in Wilcox's (1936) key to the genus and described and figured by Lavigne and Holland (1969). *S. trifasciatus* also perched on rocks in the dry streambed near Portal; south of Animas it was in a dry, sandy wash.

S. catulus was censused every half hour during five separate days during the period of 21–26 May 1980. The total number of flies seen was recorded, as were

their activity and location with respect to the stream. Location was assigned to one of the following categories: on a rock at mid-stream; on a rock surrounded by water but near the stream's edge; on a rock at streamside with water along some edge; or on rocks which were completely land-locked. Also recorded were the sex and number of individuals with prey, and instances of copulation, including duration (whether more or less than 1 min). Other intraspecific behavioral interactions were noted and distinguished according to the sexes of the participants: male–female, female–female, or male–male. A total of 60 censuses were made in this manner with the activity and location of 2453 individuals recorded. Orientation of individuals with respect to the sun was measured by compass readings for 75 individuals at 1030 and again at 1400 hr on May 26, 1980. Flies with prey were collected when possible using a clear plastic vial with snap lid along stretches of stream not used for censuses or behavioral observations. Samples were stored in small glass vials and labeled with the date, time and location of collection. A total of 90 collections were made in this manner between May 18–27, 1980. Qualitative observations were also recorded on the foraging and reproductive behavior, and on the inter- and intraspecific activities displayed by this species. Fly and prey specimens were subsequently identified and measured for body length excluding wings. Prey length was used as an index of prey size, and size data were analyzed statistically.

Results and Discussion

Daily activity rhythms.—Diurnal patterns in the activity of *S. catulus* are shown in Figure 1. In this species, as in most Asilidae that have been studied (e.g., Lavigne and Dennis, 1975), different activities seem to occur during specific periods of the day. Foraging behavior predominates in the morning hours and intraspecific interactions and copulatory behavior in the afternoon hours, similar to the pattern described for *Holopogon albipilosis* (Lavigne and Dennis, 1975) and *Nannocyrtopogon neoculatus* (Hespenheide, 1978). Overall levels of activity are greater, perhaps because of higher temperatures and greater metabolic activity. Dennis and Lavigne (1975), following Holling, have proposed that activities other than foraging are not engaged in until the flies have become food-satiated, and therefore can be expected to increase only after feeding. Increased intraspecific activity may be a necessary precursor to reproductive activity; Hinde (1970) talks of such behavior as "primer activity," i.e., activities which serve to stimulate and increase the levels of subsequent activities.

Activity levels displayed by Asilidae are typically influenced by air and substrate temperatures and availability of sunlight. Because of their dependence upon sun, asilids often remain sluggish and unable to fly until minimum air and substrate temperatures are attained. Activity levels increase but then may again be curtailed by hot midday temperatures (Lavigne and Holland, 1969). Levels of activity increase again as afternoon temperatures cool, but often not to the extent achieved at mid-morning temperatures (Hespenheide, 1978). Wind (Lavigne and Holland, 1969) and cloudy weather (Dennis and Lavigne, 1975) also effectively limit robber fly behavior. The behavior of *S. catulus* on May 24th and 25th demonstrate the importance of these factors. After the particularly cool and very windy night of 23–24 May very few flies were present in the morning hours (not censused), in strong contrast with the high levels of activity normally observed at this time

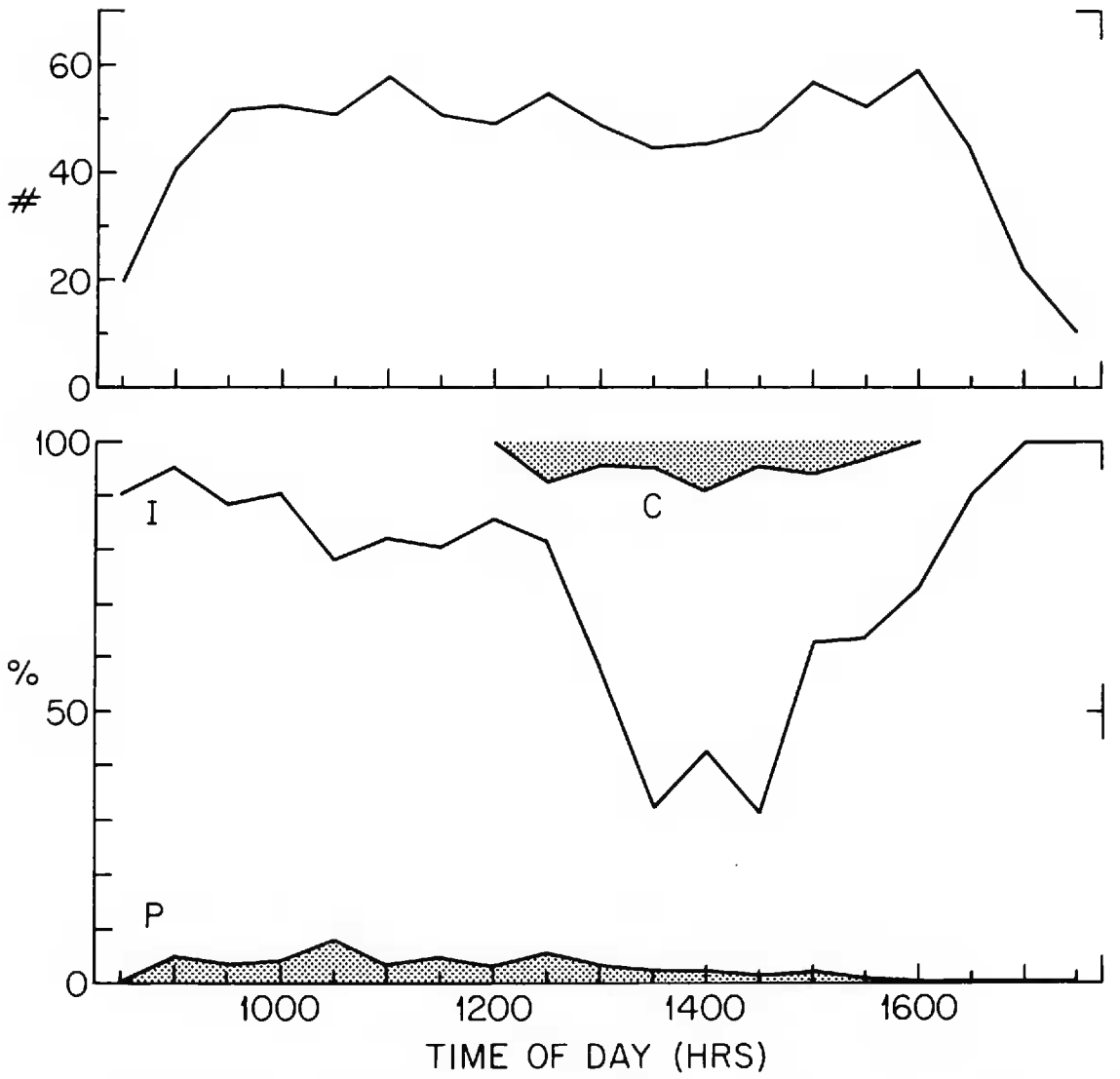

Figure 1. Numbers of flies active in censuses (upper figure) and types of activity of *Stichopogon catulus* (lower figure; P = feeding on prey, I = involved in intraspecific encounters, C = copulating—remaining flies are resting or foraging).

(Fig. 1). The afternoon of 24 May was also windy and cooler than normal; although the number of individuals observed in the late afternoon (1430–1530) was not substantially smaller than normal, the numbers of individuals diminished and activity was curtailed at an earlier time than normal when winds increased. May 25th was also preceded by a very cool night and was characterized by cool temperatures and hazy sunshine which eventually became completely overcast by 1500 hr. Activity levels were reduced during both the morning and afternoon, but not to the same extent as on the very windy day of 24 May.

Lavigne and Holland (1969) report asilids thermoregulating behaviorally through positional changes, seen also in *S. catulus*. During the cool early morning hours individuals flatten themselves to rocks, thereby maximizing the surface area in contact with the relatively warm substrate. Later in the day, as air and substrate temperatures rise, individuals stand stiff-legged on the rocks in order to minimize contact with and maximize distance from the warm substrate.

Location.—Stichopogon catulus and *S. trifasciatus* are distinctive in foraging from exposed rocks in and along streams. Lavigne and Holland (1969) describe the biology of two species of *Lasiopogon* which also forage from rocks in streams, as does a third species at Cave Creek Canyon (*Philonicus limpidipennis* (Hine)). *S. catulus* even foraged from rocks which were wet from splashing water and where it appeared an individual might easily be dislodged into the stream. This

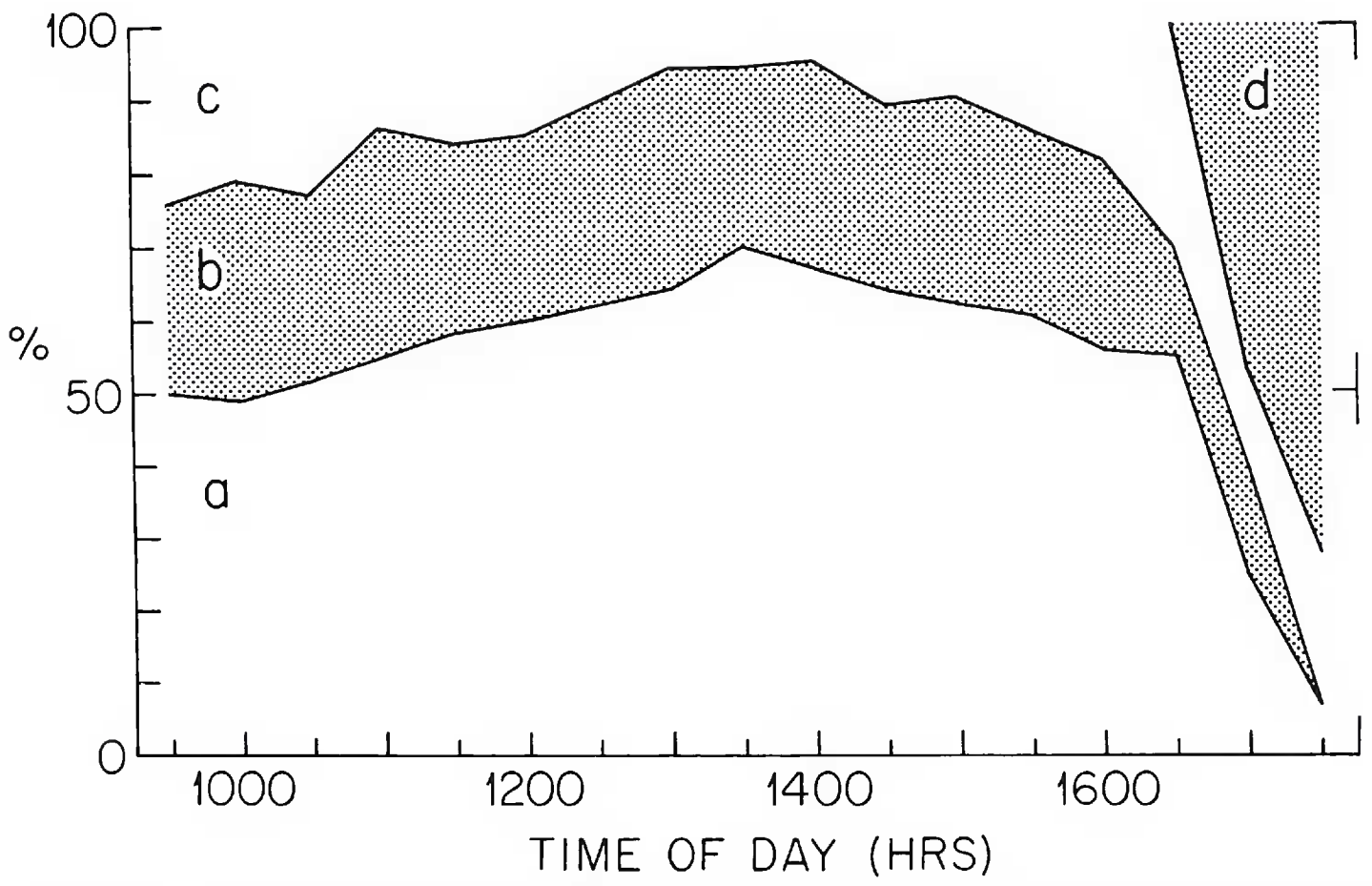

Figure 2. Diurnal changes in location of rock perches of foraging *Stichopogon catulus*: a. in mid-stream; b. surrounded by water but at edge of stream; c. bordering stream, water touching only part of rock; d. away from stream.

foraging preference is reflected in the presence of water strider nymphs (Gerridae) among the prey items (see below) although most prey were captured aerially. Although *S. catulus* tended to leave portions of the stream that dried up during the course of this study, Eric Fisher (pers. comm.) has collected the species in dry streambeds elsewhere.

Although *S. catulus* was always found on rocks in or adjacent to the stream, locational preferences changed during the day. Figure 2 shows that exposed rocks found in the middle of the stream are the preferred foraging base (except for in the very late afternoon). Exposed rocks near the stream's edge, but still surrounded by water, do not seem to be strongly preferred or avoided, except that they, too, are not used in the later afternoon. Rocks which border the stream's edge are used most frequently in the early- to mid-morning and late afternoon hours, and used least frequently during the heat of the day. When the stream has become completely shaded in the late afternoon (1630), rocks located away from the stream (1–3 m) in the dry streambed are the most heavily used, but during the remainder of the day are completely unused. It is not known whether these locational preferences change during the day for reasons having to do with thermoregulation or prey availability.

Orientation.—Background lighting by the sun has been proposed as an important mechanism by which asilids notice and recognize prey items (Dennis and Lavigne, 1975). Measurements of the orientation of foraging flies with respect to the sun indicate that they track the sun and therefore support the idea of background lighting as an important mechanism in prey location (Fig. 3). When changing their position on the rocks or flying to different rocks, the flies always appear

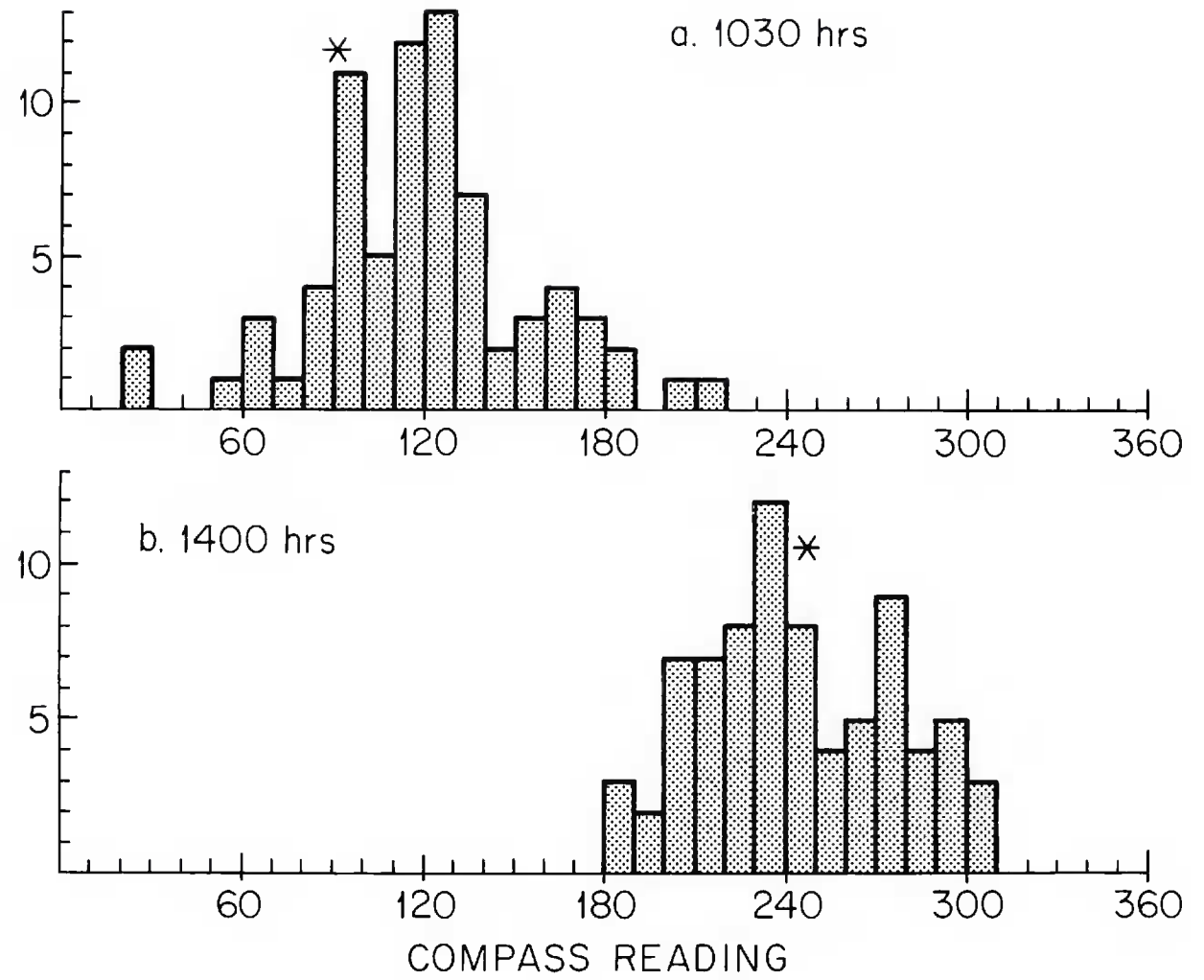

Figure 3. Orientation of foraging *Stichopogon catulus* with respect to sun at different times of day. Asterisk indicates direction of sun.

to attempt to face out over the water in the direction of the sun. Moreover, few individuals were observed on the south side of the stream, where an individual would have to look away from the sun in order to look out over the stream.

Courtship and mating behavior.—Stichopogon catulus does not appear to have a courtship display. Males usually land within a few centimeters of a female, sit for 0.5–2 min and then pounce on that female. This behavior was observed between 1030 to 1630 hr. Females usually respond with some form of rejection, either by flying off, by flying at and attacking the male, or by parting the wings and raising the abdomen. The latter display is often used by disinterested females even in the absence of an attempted copulation, apparently as a display to males in the immediate vicinity, and has been discussed by Dennis and Lavigne (1975) for *Holopogon albipilosus.* Foraging behavior and rejection were more common in the morning hours and, as Figure 1 shows, mating success was greater in the afternoon, which suggests that activities other than feeding, including copulation, are more likely to occur if the organism has fed.

Copulation is achieved only when the male is allowed by the female to mount; however, because females frequently raise their abdomen in rejection after a male has mounted, even a successful mounting does not assure successful copulation. Sexual connection is made by the male's curving his abdomen under himself until contact is made with the female's genitalia. During copulation the smaller male straddles directly over the female's abdomen (Fig. 4). The male's front tarsi are occasionally observed on the female's wings; these are usually folded over her

Figure 4. Copulating pair of *Stichopogon catulus*.

abdomen, but occasionally spread. The male's wings are always folded over his abdomen.

During copulation the pair is often interrupted by other males, who either land on the male, or more commonly land in between the copulating pair facing in the opposite direction, turn around, and attempt to displace the genitalia of the copulating male with that of his own (21 instances recorded; many others observed). If a pair *in copulo* has been connected for less than a minute, displacement is frequent, resulting in the two males' flying off in pursuit of one another. If copulation has been in progress for a greater length of time, displacement is rarely successful, even when the male was bent over backwards by the intruding male. Such intrusions by other males often cause the copulating pair to fly off, with the female carrying the male on her back to another rock. In one instance an intruding male was observed to displace a copulating male and then successfully copulate with the female who did not react to the change of mates. Multiple matings have been reported by Bullington and Lavigne (1980), but not as a result of displacement.

During copulation females are often observed with a prey item (also reported by Lavigne et al., 1976). Females preoccupied with prey are observed to be more receptive or to react less strongly or frequently to the actions of mounting males. Copulating pairs are often observed grooming their abdomen and facial areas, particularly in the final minutes before disengagement (also reported by Lavigne, 1963 and Lavigne and Holland, 1969). Length of copulation varied between less than one to as much as 16 min with most observed instances lasting less than a

Table 1. Sizes of prey of *Stichopogon catulus*.

Prey type	Males			Females			All[1]		
	n	$\bar{x}$	SD	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD
Diptera	26	2.81	0.835	30	2.92	0.923	60	2.85	0.860
Hemiptera	2	2.10	0.141	5	2.21	0.622	8	2.15	0.483
Ephemeroptera	—	—	—	4	3.27	0.134	4	3.27	0.134
Homoptera	—	—	—	4	2.40	0.496	4	2.40	0.496
Trichoptera	1	4.15	—	1	3.65	—	2	3.90	0.295
Coleoptera	—	—	—	1	2.10	—	1	2.10	—
Lepidoptera	—	—	—	—	—	—	1	2.80	—
Total	29	2.81	0.850	47	2.79	0.858	90	2.76	0.820

[1] Sex of predator was not recorded in every case.

minute. Windy and/or cloudy weather seems to significantly restrict these activities.

Foraging behavior.—Foraging and feeding behavior of *S. catulus* is very similar to that described for *Lasiopogon cinereus* (Lavigne and Holland, 1969). Foraging flights originate exclusively from exposed rocks in and along the stream, usually every two to three minutes. These flights are from 0.2 to 1.5 m in length from the foraging site and usually directed in about a 135 degree arc in front of the fly. Upon completion of a foraging flight, the fly frequently returns to within 5 cm of the initial perch or to the same rock (Powell and Stage, 1962; Lavigne, 1963). In order to intercept prey, flights from rocks are directed not only straight out and up, but also downward along the water surface (e.g., for water strider nymphs). One individual made approximately seven forage flights in quick succession along the water surface, being successful on the last attempt to capture a water strider nymph. Females make up to three times as many foraging flights as males, and foraging behavior is most common during the mid-morning hours (Fig. 1).

Prey.—Analysis and identification of 88 prey items (Table 1) indicates *Stichopogon catulus* is relatively specialized in the prey that it takes, with the order Diptera accounting for 73% of the prey items taken, followed by Hemiptera-Heteroptera (11%), Hemiptera-Homoptera (6%), Ephemeroptera (5%), Trichoptera (2%), and Coleoptera, Hymenoptera, and Lepidoptera (1% each). Especially interesting among the prey items, as mentioned above, were first and second instar nymphs of water striders of the genus *Gerris,* necessarily captured off the water surface. *Stichopogon trifasciatus* also takes prey off of surfaces in addition to aerial captures (Lavigne and Holland, 1969 and below).

The prey taken by this species ranged in size from 1.6 to 5.5 mm in length, with an overall mean length of 2.80 mm (s = 0.854). Prey sizes differed insignificantly between the sexes despite the sexual dimorphism in body size documented above, with males taking prey of mean length 2.81 mm (s = 0.850, $n = 29$) and females taking prey of mean length 2.79 mm (s = 0.858, $n = 47$). Relative to its own body length, this species takes rather large prey. The average predator/prey ratio from those samples collected is 2.23 ($n = 57$); the mean predator/prey ratio for males is 2.04 ($n = 27$) and for females 2.39 ($n = 30$).

Observations in the field and collections of predator/prey samples revealed that females were nearly twice as common as males among those individuals with

prey. The differences in predatory habits of the sexes has been suggested to be a result of the female's need for additional nourishment for the development of her eggs (Lavigne and Dennis, 1975, after Hobby) or that males may spend less time foraging for prey, and therefore would be found with fewer prey, because of the extra time they spend searching for and mating with females (Dennis and Lavigne, 1975). Informal observations support the latter suggestion: From midday on males were only infrequently seen making foraging flights and were rarely seen with prey, apparently because of their preoccupation with sexual behavior, which resulted in high levels of intraspecific activity (Fig. 1).

Courtship of Stichopogon trifasciatus.—Although observations of the courtship behavior of *S. trifasciatus* were brief compared with those of Lavigne and Holland (1969), some additional details not mentioned by them seem worth reporting. A generalized courtship sequence begins with a male joining a female on a rock perch in a face-to-face orientation and at a distance of ⅔ to ¾ body lengths. The male then does a flight display of short arcs back and forth in front of the female at about the same distance as when perched and only slightly above her and the substrate. He orients toward her constantly and moves at a rate of about two arcs (i.e., one complete movement back and forth) per second. While in flight the male's legs are dangled, but somewhat spread, and seem to be wiggled slightly; although difficult to see, the male's head may be tipped toward the female. From two to eight arcs are given in a 'bout,' after which the male either returns to his perch or makes a 'pounce' and attempts to copulate with the female. From one to seven bouts precede a pounce, and in the one observed successful copulation two unsuccessful pounces preceded the successful one. Unlike the case in *S. catulus,* there was no obvious rejection behavior by the female in failed pounces, although two sequences of bouts were interrupted by female grooming. Sequences of bouts ended by departure of either the male or the female or by copulation. The single observed copulation lasted from 30 to 60 sec with the male perched above the female, at the conclusion of which the male disengaged and flew off.

In some cases males would pounce on a female without preliminary flight displays (also observed by Lavigne and Holland, 1969), usually after flying from perches of more than a meter away. In one case a male made a pounce on a female which was in a face-to-face orientation (perched) with a second male. Lavigne and Holland (1969) report successful copulations attained by such 'intruding' males, which raises interesting questions for the evolution of courtship in the species, in the genus, and more generally. These must be answered by more systematic observations of marked populations.

Lavigne and Holland (1969) report *S. trifasciatus* to take prey from the substrate, and the only prey record observed for the species in this study was a spider. A female was seen to orient to a falling leaf, but little foraging or feeding was observed overall.

Acknowledgments

We would like to express our appreciation to Joe Wright and John Howard for aid in the capture of sample specimens; to Diane Calabrese, Eric M. Fisher, Joe Wright and Tom Sherry for identification of specimens; to Eric M. Fisher for comments on the manuscript; and to Tom Sherry for help with statistics. Part of this study was supported by a grant from the U.C.L.A. Academic Senate.

Literature Cited

Alcock, J. 1974. Observations on the behavior of *Mallophora fautrix* Osten Sacken. Pan-Pacific Entomol., 50:68–72.

Bullington, S. W., and R. J. Lavigne. 1980. An instance of multiple mating in *Asilus gilvipes* (Diptera: Asilidae). Pan-Pacific Entomol., 56:79–80.

Dennis, D. S., and R. J. Lavigne. 1975. Comparative behavior of Wyoming robber flies II. Science Monograph 30, Agric. Exp. Sta., Univ. Wyoming, Laramie, 68 pp.

Hespenheide, H. A. 1978. Prey, predatory and courtship behavior of *Nannocyrtopogon neoculatus* Wilcox and Martin (Diptera: Asilidae). J. Kansas Entomol. Soc., 51:449–456.

———, and M. A. Rubke. 1977. Prey, predatory behavior, and the daily cycle of *Holopogon wilcoxi* Martin. Pan-Pacific Entomol., 53:277–285.

Hinde, R. A. 1970. Animal behavior. McGraw Hill Book Co., New York.

Lavigne, R. J. 1963. Notes on the behavior of *Stenopogon coyote* Bromley with a description of the eggs. Pan-Pacific Entomol., 39:103–108.

———, and D. S. Dennis. 1975. Ethology of *Efferia frewingi.* Ann. Entomol. Soc. Amer., 68:992–996.

———, and F. R. Holland. 1969. Comparative behavior of eleven species of Wyoming robber flies (Diptera: Asilidae). Science Monograph 18, Agric. Exp. Sta., Univ. Wyoming, Laramie, 61 pp.

———, L. Rogers, and F. Lavigne. 1976. Ethology of *Efferia benedicti* in Wyoming. Proc. Entomol. Soc. Wash., 78:145–153.

Linsley, E. G. 1960. Ethology of some bee- and wasp-killing robber flies of southeastern Arizona and western New Mexico. Univ. Calif. Publ. Entomol., 16:357–392.

Martin, C. H., and J. Wilcox. 1965. Asilidae. *In* A. Stone, C. W. Sabrosky, W. W. Wirth, R. H. Foote, and J. R. Coulson, A catalog of Diptera of America north of Mexico. U.S.D.A. Agric. Res. Serv., Agric. Handb., 276:360–401.

Powell, J. A., and G. E. Stage. 1962. Prey selection by robberflies of the genus *Stenopogon,* with particular observations on *S. engelhardti* Bromley. Wasmann J. Biol., 20:139–157.

Scarbrough, A. G. 1981. Ethology of *Eudioctria tibialis* Banks (Diptera: Asilidae) in Maryland: seasonal distribution, abundance, diurnal movements, and behaviors. Proc. Entomol. Soc. Washington, 83:245–257.

Wilcox, J. 1936. Asilidae, new and otherwise, from the southwest, with a key to the genus *Stichopogon.* Pan-Pacific Entomol., 12:201–212.